# THE MIMICRY BETWEEN BRITISH SYRPHIDAE (DIPTERA) AND ACULEATE HYMENOPTERA

BRIGITTE HOWARTH[1,3], CARL CLEE[2] AND MALCOLM EDMUNDS[1]

[1]*Department of Biological Sciences, University of Central Lancashire, Preston PR1 2HE.* [2]*Liverpool Museum, National Museums and Galleries on Merseyside, William Brown St., Liverpool L3 8EN.* [3]*Present address: c/o Dr F. C. Howarth, Department of Physiology, Faculty of Medicine & Health Sciences, United Arab Emirates, P.O. Box 17666 Al Ain, United Arab Emirates.*

**Abstract.** Fifty-nine pairs of British hoverflies (Syrphidae) and bees or wasps (Hymenoptera) have been identified, which have similarities in morphology and colour pattern such that they may be examples of mimicry, with the hoverfly being a Batesian mimic of the hymenopteran. The study involved museum specimens supplemented by ecological and behavioural information in the literature, together with the experience of the insects in the field by a syrphid specialist and a hymenopteran specialist. In some cases field observations support the suggestion based on museum specimens that mimicry occurs, while in others field observations suggest that a different hymenopteran is actually the model. Two levels of similarity of hoverflies to Hymenoptera have been recognised, *specific* mimicry, where there is a detailed resemblance in colour, morphology and behaviour to one or a few species of bee or wasp, and *non-specific* mimicry, where the resemblance is more general and much less precise, often to a group of hymenopterans rather than to one species.

## INTRODUCTION

Hoverflies are widely accepted as being mimics of Hymenoptera (e.g. Kormann, 1988; Stubbs & Falk, 1983; Heal, 1979), and some authors have described the resemblance of syrphids to particular models, e.g. Dittrich *et al.* (1993) in Britain and Waldbauer (1970) in the United States. As part of an investigation into mimicry in British hoverflies (Howarth, 1998), this paper attempts to match model/mimic pairs in Britain and to investigate their habitat niches so as to establish whether the resemblance really is mimicry, and whether this kind of association played a part in the evolution of the Syrphidae. The objectives of this paper are (a) to identify possible model and mimic groups; (b) to assess whether the syrphids are likely to be genuine examples of Batesian mimicry by comparing flight period and habitat of proposed models and mimics; and (c) to assess whether some syrphids are very precise, specific mimics of particular hymenopterans while others have a more general, less detailed similarity to Hymenoptera.

## METHOD

The coloration, shape and size of all British syrphid species was compared with those of Hymenoptera, and a list was compiled of all hoverflies which have been successfully matched to a hymenopteran. These matching pairs (or groups) are possible examples of Batesian mimicry between hoverflies and hymenopteran models. Although some of the Hymenoptera listed do not occur in Britain, they all occur in Europe. These have been included because some of them may have become extinct in Britain, or because some of the Syrphidae may have colonised and become established in the British Isles in the absence of the model. Hoverfly species have been listed in the systematic order used by Stubbs & Falk (1983), including some

subsequent name changes (Kormann, 1988). The matching of syrphid species to hymenopteran species was carried out using specimens in both our personal and museum collections by a syrphid specialist (B.H.) and a hymenopteran specialist (C.C.).

## Criteria used

The following criteria were used for every species investigated:

(a) Overall morphological resemblance to Hymenoptera. Does the hoverfly have similar size, shape, hairiness, colour pattern and hue to a hymenopteran?

(b) Specific markings or body shape. Does the hoverfly have very precise similarities to one particular hymenopteran in markings and morphology (e.g. enlarged antennae)?

(c) Behavioural information where available. Does the hoverfly have any behavioural similarities to one particular hymenopteran? For example many parasitic Hymenoptera fly low over the ground searching for a prey species' nest (Richards, 1980), and some syrphids have been observed flying in a similar manner. This criterion only applies to species which have been observed in the field.

If a hoverfly fulfilled criterion (a) that there were overall similarities to a bee or wasp, but did not fulfil criteria (b) or (c), then it was classified as a general or non-specific bee or wasp mimic. If a hoverfly fulfilled criteria (a) and (b) (and perhaps (c) as well if information was available), such that it has a precise resemblance to one particular species (or group of similar species) of bee or wasp, then it was classified as a specific bee or wasp mimic. Thus if a hoverfly was simply striped yellow and black but its markings and shape do not closely resemble one particular solitary or social wasp, then it would be classified as a non-specific wasp mimic under criterion (a). But if a fly was large with similar markings and behaviour to a social wasp, then it would fulfil criteria (b) and (c) and so be classified as a specific mimic of social wasps.

Once a syrphid (or a visually similar group of syrphids) had been matched to a presumed model (Table 1 column "Hoverfly and Proposed Model Species"), flight period, geographical range and status, and adult habitat were compared from records in the literature. This is recorded in Table 1 as columns "Flight Period (Months), Geographical Range/Abundance (status)" and "Habitat and habits (adult)". A further column "Habit (syrphid larvae)" describes larval habit and habitat of all syrphids listed where it is known. Syrphid larval habit/habitat is important as many adult hoverflies do not feed in the same habitat that is used for oviposition and breeding. Behaviour of adult Hymenoptera consists mainly of preparing nest sites for their young, therefore habits/habitats of hymenopteran larvae are not described separately but are included under "Habitat and habits (adult)". The final column, "Plate No./Notes", includes any relevant personal observations and in some cases reference to a colour plate.

The column "Hoverfly and Proposed Model Species" lists a hoverfly species or genus (or a group of hoverflies which are indistinguishable in flight), and below this, separated by a line, is the proposed model species or genus. This is one model/mimic pair or group to which the unique reference number in the first column, "No.", refers. This reference number is also used in the results. Column 3, "Flight Period (Months)", refers to months by number (i.e. January is 1, February 2 etc.). The peak flight period is given in bold font.

Table 1. Fifty-nine possible examples of Batesian mimicry in the British Syrphidae
Each Number gives a model mimic pair with the mimic(s) first (above the line) and the model(s) second (below the line).
Information from Ball and Morris (in prep.), Chinery (1993, 1986), Else (in prep.), Kormann (1988), Richards (1980), Stubbs and Falk (1983), Yeo and Corbet (1983); other sources credited where appropriate.
Abbreviations in 'Geographical Range/Abundance (Status)': BI British Isles, E England, GB Great Britain, I Ireland, S Scotland, W Wales, s south, w west, n north, e east.
'Flight Period': bv bivoltine; peak season in bold.
'Plate No./Notes': † Carl Clee; *Brigitte Howarth
(for further details of columns see text).

| No. | Hoverfly and Proposed Model Species | Flight Period (Months) | Geographical Range/ Abundance (status) | Habitat and habits (adult) | Habit (syrphid larvae) | Plate No./ Notes |
|---|---|---|---|---|---|---|
| | **SYRPHINAE**<br>**BACCHINI** incl.<br>**MELANOSTOMATINI** | | | | | |
| 1. | *Baccha elongata* (Fab.), *B. obscuripennis* Meigen | **5–6, 8–9**–10 | BI, common | woodland margins and hedgerows | aphidophagous; associated with ground layer aphids | |
| | *Trypoxylon attenuatum* Smith<br>*T. clavicerum* Lep. & S. | 5–9 | *T. attenuatum* GB, common<br>*T. clavicerum* E, W, common | woodland, nests in cut stems and hollow roots, preys on spiders | | |
| 2. | *Melanostoma* spp., *Platycheirus* spp. with yellow markings | 4–11 | *Melanostoma* spp. BI, common<br>*Platycheirus* spp. BI, common | moist herbage and grassland, scrub and woodland margins | aphidophagous | Plate 1 |
| | *Crossocerus quadrimaculatus* (Fab.) | 6–9 | E, W, I, common | wooded areas, varied prey but mainly Diptera, nests in earth particularly amongst roots of uprooted trees | | Plate 1 |

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Table I. *(continued)*

| No. | Hoverfly and Proposed Model Species | Flight Period (Months) | Geographical Range/ Abundance (status) | Habitat and habits (adult) | Habit (syrphid larvae) | Plate No./ Notes |
|---|---|---|---|---|---|---|
| 3. | *Pyrophaena granditarsa* (Forster) | 5–10 | GB, I, common | marshy meadows, lush vegetation by ditches and lakes | aphidophagous | low-flying over vegetation at ground level; Plate 4 |
| | *Nomada fabriciana* (L.) | 3–6, 6–8 bv | BI, common (rare in I) | calcareous grassland, open grassland, woodland margins | | *Sphecodes* and *Nomada* also low-flying; Plate 4 |
| | *Andrena labiata* Fab. | 3–6, 6–8 bv | E; locally common | | | |
| | *Andrena marginata* Fab. | 3–9 | scattered throughout GB, rare | | | |
| | *Sphecodes spinulosus* von Hagens | 5–6 | sE, sW, rare | | | |
| | **SYRPHINI** incl. **CHRYSOTOXINI** | | | | | |
| 4. | *Chrysotoxum arcuatum* (L.), *C. cautum* (Harris), *C. elegans* Loew, *C. octomaculatum* Curtis, *C. verralli* Collin | 5–9 | *C. arcuatum* nGB, I, frequent (local); others sGB, some frequent some rare | lightly wooded areas, moorland margins | myrmecophilous, feeding on root aphids in ant nests (Rotheray *et al.*, 1996) | flies over low vegetation*; Plate 2 |
| | *Dolichovespula* spp. and *Vespula* spp. | 3/4–10 | BI, common | various habitats | | Plate 2 |
| | *Anthidium* spp. | 5–8 | sE, mainly European, common | | | |
| 5. | *Chrysotoxum bicinctum* (L.) | 5–6–9 | BI, frequent | grassy areas, meadows with shelter near scrub and trees | myrmecophilous, feeding on root aphids in ant nests (Rotheray *et al.*, 1996) | |
| | *Argogorytes mystaceus* (L.) | 5–8 (9) | BI, common | variety of habitats, preys on nymphs of *Philaenus* (Aphrophoridae), nests in soil | | |

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Table 1. *(continued)*

| No. | Hoverfly and Proposed Model Species | Flight Period (Months) | Geographical Range/ Abundance (status) | Habitat and habits (adult) | Habit (syrphid larvae) | Plate No./ Notes |
|---|---|---|---|---|---|---|
| 6. | *Chrysotoxum festivum* (L.) | 6–**7–8**–10 | GB (mainly s), I, never abundant, but frequent in sGB (local) | grassy areas near woodland or scrub margins | myrmecophilous, feeding on root aphids in ant nests (Rotheray *et al.*, 1996) | |
| | *Ectemnius cavifrons* (Thompson) | 6–10 | E, W, I, common | often seen on flowers of umbellifers, preys on Diptera (mainly Syrphidae), nests in rotten wood or plant stems | | |
| 7. | *Dasysyrphus tricinctus* (Fallén) | 4–**5–6**, **8–9**–10 | BI, common | margins of lowland woods | primarily aphidophagous (Rotheray, pers. comm.), but also predatory on tenthredinid (Gäbler, 1939) and noctuid larvae (Friederichs *et al.*, 1940) | Plate 2 |
| | *Nysson spinosus* (Forster) | 5–7 | BI, common | associates with *Argogorytes mystaceus* and *A. fargeii* | | cleptoparasitic, Plate 2 |
| 8. | *Doros profuges* (Harris) (= *conopseus* Fab.) (Rab.) | **6**–7 | GB, rare, vulnerable (scattered distribution) (Falk, 1991) | has been seen near or resting on bramble | unknown, ant association suggested (Lundbeck, 1916) | Plate 2 |
| | *Odynerus* spp. | 5–8 9 | BI, rare | nests in soil or vertical sand faces | | Plate 2 |
| | *Ancistrocerus antilope* (Panzer) | 6–8 | GB, irregular not often common | nests in a variety of cavities | | |
| 9. | *Episyrphus balteatus* (Degeer) | 1–**7–9**–12 | BI, common | varied habitats | polyphagous on ground layer and arboreal aphids | |
| | *Nomada* spp. | 3–8 | BI, common but some rare | varied habitats | | |

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Table 1. *(continued)*

| No. | Hoverfly and Proposed Model Species | Flight Period (Months) | Geographical Range/ Abundance (status) | Habitat and habits (adult) | Habit (syrphid larvae) | Plate No./ Notes |
|---|---|---|---|---|---|---|
| 10. | *Eriozona syrphoides* (Fallén) | 5, 7–**8–9**–10, bv | GB, local | spruce plantations, deciduous woods containing spruce | aphidophagous on conifer aphids (Kula, 1983) | prefers mauve flowers |
| | *Bombus pratorum* (L.) | 2–9 | BI, common | meadow, woodland margins | | |
| | *Bombus sylvarum* (L.) | 5–9 | GB (mainly s), I, rare | woodland, calcareous grassland, heathland, coastal shingle | | |
| | *Bombus terrestris* (L.) | 2–10 | BI, common | various habitats | | |
| 11. | *Melangyna* spp. incl. *Meligramma* and *Meliscaeva* spp. | 3–10 | BI, common as a group | woodland, high in canopy on sallow blossom, hazel catkins, also on ground flowers | aphidophagous, associated mainly with arboreal aphids (Rotheray, 1993) | no plate, but similar to no. 2 |
| | *Crossocerus quadrimaculatus* (Fab.) | 6–9 | E, W, I, common | see 2 | | |
| 12. | *Scaeva pyrastri* (L.) | 5–**7–8**–11 | BI, frequent but fluctuates (migrant) | meadows, gardens, waste ground | aphidophagous, primarily associated with ground layer aphids (Rotheray, 1993) | Plate 3 |
| | *Bembix rostrata* (L.) | 6–8 | European species | European species, preys on Diptera | | Plate 3 |
| 13. | *Sphaerophoria* spp. | 4–10 | BI, common as a group | dry grassland, woodland rides or marshes | aphidophagous on ground layer aphids (Rotheray, 1993) | |
| | *Cerceris quinquefasciata* (Rossius) | 7–8 | sE, rare | nests in sand, preys on Coleoptera | | |
| | *Crossocerus quadrimaculatus* (Fab.) | 6–9 | E, W, I, common | see 2 | | |
| | European *Ectemnius* | 6–8 | European spp. | ground, plant stems and rotten wood nesting | | |

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Table 1. *(continued)*

| No. | Hoverfly and Proposed Model Species | Flight Period (Months) | Geographical Range/ Abundance (status) | Habitat and habits (adult) | Habit (syrphid larvae) | Plate No./ Notes |
|---|---|---|---|---|---|---|
| 14. | *Syrphus* spp. | 3–11 | BI, common | various habitat areas | aphidophagous (Rotheray, 1993) | |
| | *Dolichovespula* spp. and *Vespula* spp. | 3/4–10 | BI, common | various habitats | | |
| 15. | *Xanthogramma citrofasciatum* (Degeer) | 4–5–early 7 | E (mainly s), scarce (local) | meadows, dry grassland | myrmecophilous, feeding on root aphids in ant nests (Rotheray *et al.*, 1996) | hovers low over ground;* Plate 4 |
| | *Nomada goodeniana* (Kirby) | 4–7, 7–8, bv | BI, common (rare in I and S) | hedge and ditch banks, usually dry ground | | *Ectemnius* spp. prey on syrphids; Plate 4 |
| | *Nomada marshamella* (Kirby) | 4–6, 6–9, bv | BI, common | as above | | |
| | *Nomada fulvicornis* Fab. | 3–6, 6–8, bv | GB (mainly sE), rare | as above | | |
| | *Ectemnius* spp. | 5–10 | BI, some common, some rare | nests in rotten wood on plant stems | | |
| 16. | *Xanthogramma pedissequum* (Harris) | 5–6–8–9 | E, W, scarce (mainly s) (local) | grassland and open woodland rides | myrmecophilous, feeding on root aphids in ant nests (Rotheray *et al.*, 1996) | hovers low over ground;* Plate 4 |
| | *Crabro cribrarius* (L.) | 5–9 | BI, common | nests in soil, preys on Diptera incl. syrphids | | Plate 4 |
| | *Ectemnius* spp. | 5–10 | see no. 15 | see 6 | | |
| | *Nomada* spp. | 4–9 | see no. 15 | varied habitat | | |

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Table 1. *(continued)*

| No. | Hoverfly and Proposed Model Species | Flight Period (Months) | Geographical Range/ Abundance (status) | Habitat and habits (adult) | Habit (syrphid larvae) | Plate No./ Notes |
|---|---|---|---|---|---|---|
| | **MILESIINAE** | | | | | |
| | **CALLICERINI** | | | | | |
| 17. | *Calicera aenea* (F.), *C. rufa* Schummel, *C. spinolae* Rondani | 6–10 | *C. aenea* sE, rare<br>*C. rufa* S, rare<br>*C. spinolae* sE, endangered (Falk, 1991) | found in ancient pine woods known from East Anglia | saprophagous, larvae in this genus found in rot-holes (Rotheray, 1993) | Plate 3 |
| | *Osmia* spp. | 4–8 | BI, frequent | burrows in soil, cavities in dead wood or snail shells | | Plate 3 |
| | *Anthophora* spp. | 6–9 | BI, frequent | burrows in level soil, sandy banks, cliff faces, lowland heaths and coastal dunes | | |
| | *Eucera longicornis* (L.) | 4–7 | E, W locally common | flower-rich sandy habitats | | |
| | **CHEILOSIINI** | | | | | |
| 18. | *Cheilosia albipila* Meigen | 3–**4**–6 | BI, frequent (local) | sallow, hazel catkins, ferns, marshes, wet meadows | phytophagous on *Cirsium palustre* stems (Andrewes, 1944, and Rotheray, 1988) | fly and bee seen together on sallow† |
| | *Andrena apicata* Smith | 3–5 | BI, frequent (common in s) | open woodland, heaths, moorland and abandoned sand and chalk quarries; sallow specialist | | |
| 19. | *Cheilosia chrysocoma* (Meigen) | 3–**5**–6 | GB, I, S, W, rare | woodland rides, glades, and edges, close to marshy areas | phytophagous, plant unknown (Stubbs and Falk, 1983) | Plate 3 |
| | *Andrena fulva* Müller | 3–6 | BI, common (mainly E, W) | level ground with short grass | | nests in coastal clay cliffs†; Plate 3 |
| | *Osmia rufa* (L.) | 4–5/6/7 | GB, common | cavities in sandy soils, dead wood, crevices | | |

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Table 1. *(continued)*

| No. | Hoverfly and Proposed Model Species | Flight Period (Months) | Geographical Range/ Abundance (status) | Habitat and habits (adult) | Habit (syrphid larvae) | Plate No./ Notes |
|---|---|---|---|---|---|---|
| 20. | *Cheilosia grossa* (Fallén) | 3–**late 3–4**–5 | BI, scarce (local) | woodland rides, glades and edges, grazing marshes, wet meadows. On sallow and hazel | phytophagous on *Cirsium palustre*, *C. vulgaris* and *Carduus tenuiflorus* in stem and root (Rotheray, 1993) | |
| | *Andrena nigroaenea* (Kirby) | 3–5/6, 7/8 | BI, common | frequents sallow and dandelion, nests in sandy loamy soil | | |
| 21. | *Cheilosia impressa* Loew, *C. mutabilis* (Fallén), *C. nebulosa* Verrall, *C. pagana* (Meigen), *C. vernalis* (Fallén) | 3–9 | *C. pagana* and *C. vernalis* BI, common, others rare | varies from damp woods to open grassland, usually on low flowers and umbellifers | phytophagous (Rotheray, 1993) | small black or brown |
| | *Lasioglossum albipes* (Fab.), *L. fratellum* (Perez) | 4–10 | BI, common | | | small black or brown |
| 22. | *Cheilosia illustrata* (Harris) | 4–**7–8**–9 | BI, common | woodland, woodland margins, umbellifers | phytophagous on *Heracleum sphondylium* and *Angelica sylvestris* (Stubbs and Falk, 1983) | general bumble bee mimic* |
| | *Andrena cineraria* (L.) | 3–6 | BI, common, scarce in seE, S | pasture land, woodland, chalk grassland and coastal sites | | |
| | *Bombus pratorum* (L.) | 2–9 | BI, common | see 10 | | |
| 23. | *Ferdinandea cuprea* (Scopoli) | 4–**5–6**–10 | BI, frequent (local) | woodland, tree trunks or dead leaves in dappled light | saprophagous, found in sap-runs on deciduous trees (Rotheray, 1993) | |
| | *Andrena apicata* Smith | 3–4, also 5 | BI, frequent (common in s) | see 18 | | |
| | *Osmia rufa* (L.) | 4–7 | GB, common | see 17 and 19 | | |

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Table 1. *(continued)*

| No. | Hoverfly and Proposed Model Species | Flight Period (Months) | Geographical Range/ Abundance (status) | Habitat and habits (adult) | Habit (syrphid larvae) | Plate No./ Notes |
|---|---|---|---|---|---|---|
| 24. | *Rhingia campestris* Meigen | 4–**5–6+9**–11, | BI, common | open woodland, woodland edges, hedgerows | saprophagous, in cow dung (Coe, 1942) | |
| | *Andrena marginata* Fab. | 3–9 | scattered throughout GB, rare | see 3. | | |
| | *Sphecodes gibbus* (L.) | 4–9 | GB, common | light sandy soils, woodland edges | | |
| | **CHRYSOGASTRINI** | | | | | |
| 25. | *Neoascia geniculata* (Meigen), *N. interrupta* (Meigen), *N. meticulosa* (Scopoli), *N. obliqua* Coe, *N. podagrica* (F.), *N. tenur* (Harris) | 4–**5–6+7–9**–11 | BI, common as a group, some are rare | near marshes, water edges, hedgerows, woodland margins | saprophagous, found in decaying vegetation round the margins of ponds (Rotheray, 1993) | |
| | *Stigmus solskyi* Morawitz | 6–8 | E, W, scarce | in small beetle holes in wood and cut stems | | *S. solskyi* varies in size |
| | *Crossocerus megacephalus* (Rossius), *C. ovalis* Lepeletier & Brulle, *C. elongatulus* (Vander Linden), *C. wesmaeli* (Vander Linden) | 5–9 | BI, common | wooded areas, varied prey but mainly Diptera, nests in earth particularly amongst roots of uprooted trees | | |
| 26. | *Sphegina clunipes* (Fallén), *S. kimakowiczi* Strobl, *S. verecunda* Collin | **5–7**–10 | BI, frequent (*S. clunipes*) (local) | deciduous woodland with lush herb layer, damp shady woodland | saprophagous, in decaying sap under bark, usually in wet situations (Rotheray, 1993) | |
| | *Pemphredon inornata* Say | 5–9 | BI, common | woodland, nests in stems | | |
| | *Pemphredon lethifera* (Shuckard) | 5–10 | BI, common | woodland, nests in cut stems, usually *Rubus* | | |
| | *Psenulus pallipes* (Panzer) | 5–8 | E, W, I, common | nests in stems, straw, beetle holes in wood, preys on aphids | | |

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Table 1. *(continued)*

| No. | Hoverfly and Proposed Model Species | Flight Period (Months) | Geographical Range/ Abundance (status) | Habitat and habits (adult) | Habit (syrphid larvae) | Plate No./ Notes |
|---|---|---|---|---|---|---|
| | **ERISTALINI** | | | | | |
| 27. | *Anasimyia contracta* Claussen & Torp, *A. transfuga* (L.) | 5–**6–7**–8 | sE, W, I, S, frequent but local | margins of ditches, ponds and lakes | rat-tailed larva, in pools/ ponds with *Typha* and decaying vegetation (Rotheray, 1993) | |
| | *Epecolus variegatus* (L.) | 6–8 | GB (mainly s), locally common | open woodland, coastal dunes | | |
| | *Epecolus cruciger* (L.) | 6–9 | GB (mainly s), locally common | heathland and coastal dunes | | |
| 28. | *Anasimyia lineata* (Fab.) | 5–**6–7**–9 | BI, frequent but local | bogs | rat-tailed larva, as 27 | |
| | *Coeliozys inermis* (Kirby) | 5–8 | sE, W, locally common | cleptoparasitic on *Megachile* and *Anthophora*, found near sand dunes | | |
| 29. | *Eristalis arbustorum* (L.) | **4–7–9**–11 | BI, common | open habitats, woodland and field margins | rat-tailed larva in farmyard drains, and decaying vegetation (Rotheray, 1993) | Plate 4 |
| | *Apis mellifera* L. | 3–10/11 | BI, common | various habitats | | Plate 4 |
| | *Andrena flavipes* Panzer | 3–6, 6–9, bv | GB (mainly s), frequent | open woodland, chalk grassland, coastal landslips | | |
| | *Stelis punctulatissima* (Kirby) | 5–8 | sGB, rare | dead wood, beetle holes, cuckoo of *Osmia* spp. | | |
| 30. | *Eristalis intricarius* (L.) | 3–**7–8**–10 | BI, common | flowers, marshy woodland and margins | saprophagous, as 29 | Plate 5 |
| | *Bombus terrestris* (L.) | 2–10 | BI, common | various habitats | | Plate 5 |
| | *Bombus pratorum* (L.) | 2–9 | BI, common | see 10 | | |

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Table 1. *(continued)*

| No. | Hoverfly and Proposed Model Species | Flight Period (Months) | Geographical Range/ Abundance (status) | Habitat and habits (adult) | Habit (syrphid larvae) | Plate No./ Notes |
|---|---|---|---|---|---|---|
| 31. | *Eristalis pertinax* (Scopoli), *E. rupium* Fab., *E. tenax* (L.) | 1–12 | BI, common | various habitats | saprophagous, as 29 | |
| | *Apis mellifera* L. | 3–10/11 | BI, common | various habitats | | |
| 32. | *Helophilus* spp. | 4–11 | BI, common | pond or ditch margins, muddy puddles, meadows. At flowers | saprophagous, as 29 | |
| | *Dolichovespula* spp. and *Vespula* spp. | 3/4–10 | BI, common | various habitats | | |
| 33. | *Lejops vittata* (Meigen) | 5–**7–8**–9 | sE, rare, vulnerable (Falk, 1991) | coastal and other marshes | long-tailed larva (Rotheray, pers. comm.), not described | low flight; Plate 3 |
| | *Coelioxys inermis* (Kirby) and other *Coelioxys* spp. | 5–8 | sE, W, locally common | cleptoparasitic on *Megachile* and *Anthophora*, found near sand dunes | | low flight over ground; Plate 3 |
| 34. | *Mallota cimbiciformis* (Fallén) | 5–**6–8**–9 | E, rare, notable (Falk, 1991) | forests, parks | saprophagous, in rot holes in trees (Rotheray, 1993) | Plate 1 |
| | *Apis mellifera* L. | 3–10/11 | BI, common | see 31 | | Plate 1 |
| 35. | *Myathropa florea* (L.) | 5–10 | BI, common | wooded areas | saprophagous, as 34 | |
| | *Dolichovespula* spp. and *Vespula* spp. | 3/4–10 | BI, common | various habitats | | |
| 36. | *Parhelophilus frutetorum* (Fab.) | 5–**6–7**–8 | sGB, locally frequent | open pond sites and ditches with *Typha* | saprophagous, associated with accumulations of decaying vegetation (Rotheray, 1993) | Plate 2 |
| | *Vespula rufa* (L.) | 2–**4–6**–10 | BI, common | subterranean nests, found widely distributed | | Plate 2 |

*(continued on next page)*

Table 1. *(continued)*

| No. | Hoverfly and Proposed Model Species | Flight Period (Months) | Geographical Range/ Abundance (status) | Habitat and habits (adult) | Habit (syrphid larvae) | Plate No./ Notes |
|---|---|---|---|---|---|---|
| | **MERODONTINI** | | | | | |
| 37. | *Eumerus sabulonum* (Fallén) | 5–6–9 | wE, wS, wW, rare, notable (Falk, 1991) | sand dunes and earthy coastal cliffs | probably feed on fungal breakdown products within pockets of decay in live or recently dead herbaceous plants (Rotheray, 1993) | |
| | *Nysson dimidiatus* Jurine | 6–9 | E, W. scarce | cleptoparasitic on *Gorytes tumidus* or *Lindenius albilabris* | | this could be aggressive mimicry*; Plate 5 |
| | *Gorytes tumidus* (Panzer) | 6–9 | Bl, scarce | nests in sand, preys on Hemiptera | | |
| 38. | *Eumerus strigatus* (Fallén), *E. tuberculatus* Rondani | 3–~~4–5~~+ **8–9**–10 | Bl, common | various habitats | phytophagous on plant bulbs, with fungal decay present (Creager and Spruijt, 1935) | Plate 5 |
| | *Osmia caerulescens* (L.) | 4–8 | E, W, common | various habitats | | Plate 5 |
| | *Hoplitis claviventris* (Thomson) | 5–8 | E, W, frequent, locally common | calcareous grassland, open woodland, dunes | | |
| | *Stelis ornatula* (Klug) | 5–8 | E, as far n as Midlands | dead wood, beetle holes | | |
| 39. | *Merodon equestris* (Fab.) | 4–late 5–6–8 | Bl, locally common | woodland with *Narcissus* bulbs | phytophagous on bulbs of *Narcissus* flowers (Hodson, 1932) | polymorphic, many forms |
| | *Bombus terrestris* (L.), *B. lucorum* (L.), *B. muscorum* (L.), *B. pascuorum* (Scopoli), *B. ruderarius* (Müller) | 2–11 | Bl, common | various habitats | | |

*(continued on next page)*

Table 1. *(continued)*

| No. | Hoverfly and Proposed Model Species | Flight Period (Months) | Geographical Range/ Abundance (status) | Habitat and habits (adult) | Habit (syrphid larvae) | Plate No./ Notes |
|---|---|---|---|---|---|---|
| | **SERICOMYIINI** | | | | | |
| 40. | *Arctophila superbiens* (Müller) (= *A. fulva*) | 7–**8–9**–11 | BI, frequent but local (mainly n + w) | woodland margins, meadows with *Succisa* flowers | saprophagous; wet decaying vegetation on moorlands (Rotheray, pers. comm.) | |
| | *Bombus muscorum* (L.), *B. pascuorum* (Scopoli) | 4–**7–9**–10 | BI, common | various habitats | | |
| 41. | *Sericomyia lappona* (L.) | 4–8 | BI, local | boggy localities, woodland margins with river nearby, boggy meadows | saprophagous; wet decaying vegetation on moorlands (Rotheray, 1993) | Plate 4 |
| | *Anthophora quadrimaculata* (Panzer) | 6–8 | sE, scarce but locally common | rural and urban areas, sandy banks and cliffs | | Plate 4 |
| | *Andrena flavipes* Panzer | 3–5, 6–9, bv | GB (mainly s), frequent | see 29 | | |
| | *Andrena labialis* (Kirby) | 5–8 | E, sW, frequent | deciduous woodland, fenland, grasslands | | |
| 42. | *Sericomyia silentis* (Harris) | 5–9 | BI, common | boggy heaths, acid wet meadows or woodland clearings/ margins | saprophagous; wet decaying vegetation on moorlands (Rotheray, 1993) | |
| | *Dolichovespula* and *Vespula* spp. | 3/4–10 | BI, common | various habitats | | |

*(continued on next page)*

Table 1. *(continued)*

| No. | Hoverfly and Proposed Model Species | Flight Period (Months) | Geographical Range/ Abundance (status) | Habitat and habits (adult) | Habit (syrphid larvae) | Plate No./ Notes |
|---|---|---|---|---|---|---|
| | **VOLUCELLINI** | | | | | |
| 43. | *Volucella bombylans* (L.) | 5-**6**-8 | BI, common | woodlands and meadows with woodland nearby | found in vespine nests, thought to feed on debris, possibly predatory on host larvae (Rotheray, 1993) | polymorphic, with three forms; Plate 5 |
| | *Bombus lapidarius* (L.), *B. lucorum* (L.), *B. ruderarius* (Müller), *B. terrestris* (L.) and possibly *B. pascuorum* (Scopoli) (pale variety) | 2–11 | BI, frequent as a group | various habitats | | Plate 5 |
| 44. | *Volucella inanis* (L.) | 7–**8**–10 | sE, frequent, notable (Falk, 1991) | on Continent in woodland and margins | ectoparasite of vespine larvae (Rupp, 1989) | recent colonist |
| | *Vespula* spp.<br>*Vespa crabro* L. | 3/4–10<br>5–9 | BI, common<br>sE, locally common | various habitats<br>nests in hollow trees, food ineludes nectar, fruit, insects | | |
| 45. | *Volucella zonaria* (Poda) | 6–**8**–10 | sE, frequent, notable (Falk, 1991) | on Continent near woodland meadows and margins | found in vespine nests, may feed on debris or predatory on host larvae (Rotheray, 1993) | recent colonist |
| | *Vespa crabro* L. | 5–9 | sE, locally common | see 44 | | |

*(continued on next page)*

Table 1. *(continued)*

| No. | Hoverfly and Proposed Model Species | Flight Period (Months) | Geographical Range/ Abundance (status) | Habitat and habits (adult) | Habit (syrphid larvae) | Plate No./ Notes |
|---|---|---|---|---|---|---|
| | **XYLOTINI** | | | | | |
| 46. | *Blera fallax* (L.) | 6–8 | S, rare, endangered (Falk, 1991) | pine forests of the eastern Highlands, Scotland | found in rot-holes of *Pinus* (Rotheray and Stuke, 1998) | Plate 5 |
| | *Osmia bicolor* (Schrank) | 4–7 | sE, W, scarce | calcareous grassland, also open woodland (southern species), nesting in snail shells | | Plate 5 |
| | *Osmia aurulenta* Fab. | 4–8 | BI, locally common in s | coastal, inland confined to calcareous grassland, nesting in snail shells | | |
| 47. | *Brachypalpoides lenta* (Meigen) | **5–6**–8 | E, W, S, I, scarce (local) | forested districts | saprophagous, decaying heartwood of *Fagus* (Rotheray, 1993), and other trees (Rotheray, pers. comm.) | resembles a saw-fly*, Plate 1 |
| | *Astata boops* (Schrank) | 6–8 | seE, common | dry sandy banks and habitats, sometimes on umbellifers | | Plate 1 |
| 48. | *Brachypalpus laphriformis* (Fallén) | 4–**5–6**–8 | E, S, W, rare | ancient woodland/woodland margins | saprophagous, in rot-holes of deciduous trees (*Quercus*) (Rotheray, 1993) | Plate 1 |
| | *Colletes* spp. | 6–10 | BI, common | various habitats, also open woodland | | |
| | *Apis mellifera* L. | 3–10/11 | BI, common | various habitats | | Plate 1 |

*(continued on next page)*

Table 1. *(continued)*

| No. | Hoverfly and Proposed Model Species | Flight Period (Months) | Geographical Range/ Abundance (status) | Habitat and habits (adult) | Habit (syrphid larvae) | Plate No./ Notes |
|---|---|---|---|---|---|---|
| 49. | *Caliprobola speciosa* (Rossi) | 5–**6**–7 | sE, rare, notable (Falk, 1991) | deciduous woodland | saprophagous, in decaying heartwood of *Fagus* trees, particularly old stumps (Rotheray, 1993) | |
| | *Dolichovespula sylvestris* (Scopoli), *D. media* (Retzius) | 3–9 | BI, common | nests underground but also in ivy, hollow trees, beehives, trees or bushes | | |
| 50. | *Chalcosyrphus (Xylotina) nemorum* (Fab.) | **4**–**5**–**7**–9 | BI, scarce (can be common in s) (local) | ancient woodland | saprophagous; under bark in decaying sap (Rotheray, 1993) | |
| | *Crabro scutellatus* (Scheven) | 6–8 | E, frequent but local | in soil and preys on Diptera | | |
| | *Ectemnius continuus* (Fab.) | 5–9 | BI, common | in rotten wood, plant stems, prey as above | | |
| 51. | *Chalcosyrphus (Xylotodes) cunotus* (Loew) | **4**–**6**–7 | E, W, rare, vulnerable (Falk, 1991) | woodland/shaded situation by water | saprophagous, see previous species | |
| | *Colletes* spp. | 6–10 | BI, common | see 48 | | no plate but pair like no. 48 |
| | *Apis mellifera* L. | 3–10/11 | BI, common | various habitats | | |
| 52. | *Criorhina asilica* (Fallén) | **4**–**5**–7 | E, scarce, notable (Falk, 1991) | ancient woodland/woodland margins | saprophagous, decaying heartwood, old stumps and rot-holes (Rotheray, 1993) | Plate 1 |
| | *Apis mellifera* L. | 3–10/11 | BI, common | various habitats | | Plate 1 |

*(continued on next page)*

Table 1. *(continued)*

| No. | Hoverfly and Proposed Model Species | Flight Period (Months) | Geographical Range/ Abundance (status) | Habitat and habits (adult) | Habit (syrphid larvae) | Plate No./ Notes |
|---|---|---|---|---|---|---|
| 53. | *Criorhina berberina* (F.) | 4–**5**–**6**–8 | E, I, W, S, frequent (local) | ancient woodland/woodland margins | saprophagous, as 52 | |
| | *Bombus pascuorum* (Scopoli), *B. pratorum* (L.), *B. terrestris* (L.) | 2–11 | BI, common | various habitats | | |
| 54. | *Criorhina floccosa* (Meigen) | 4–**5**–**6**–7 | BI, scarce (local) | ancient woodland/woodland margins | saprophagous, as 52 | |
| | *Bombus muscorum* (L.), *B. pascuorum* (Scopoli) | 3–11 | BI, common | various habitats | | |
| 55. | *Criorhina ranunculi* (Panzer) | **3**–**5**–6 | BI, scarce, notable (Falk, 1991) | ancient woodland/woodland margins, often found feeding on *Salix* spp. | saprophagous, as 52 | Plate 5 |
| | *Bombus lapidarius* (L.), *B. lucorum* (L.), *B. ruderarius* (Müller), *B. terrestris* (L.) | 2–10 | BI, common | various habitats | | Plate 5 |
| 56. | *Pocota personata* (Harris) | 4–**6**–7 | E, scarce, vulnerable (Falk, 1991) | mostly a southern species | saprophagous, breeds in rot-holes (Rotheray, 1993) | Plate 5 |
| | *Bombus terrestris* (L.) | 2–10 | BI, common | various habitats | | Plate 5 |
| 57. | *Syritta pipiens* (L.) | 4–**7**–**9**–10 | BI, common | rough meadows, hedgerows, marshy areas | saprophagous, in wet, decaying matter incl. compost, manure, silage (Rotheray, 1993) | |
| | *Crossocerus quadrimaculatus* (Fab.) | 6–9 | E, W, I, common | see 2 | | |

*(continued on next page)*

Table 1. *(continued)*

| No. | Hoverfly and Proposed Model Species | Flight Period (Months) | Geographical Range/ Abundance (status) | Habitat and habits (adult) | Habit (syrphid larvae) | Plate No./ Notes |
|---|---|---|---|---|---|---|
| 58. | *Tropidia scita* (Harris) | 4–6–7–9 | E, S, I, frequent, locally abundant | open fens and lush marshes | saprophagous, decaying vegetation, mud margins (Decleer and Rotheray, 1990) | |
| | *Nomada ruficornis* (L.) | 4–6 | BI, common | various habitat areas | | |
| | *N. fabriciana* (L.) | 3–8, bv | BI, common | woodland, heaths, coast, moors, meadows | | |
| | *N. flava* Panzer | 4–6 | sE, common | hedgebanks, ditches | | |
| | **MICRODONTINAE** | | | | | |
| 59. | *Microdon mutabilis* (L.) | 5–6–7 | BI, rare, notable (Falk, 1991) | grassy limestone slopes/ woodlands/wood margins, wet meadows, dune slacks | predaceous on ant larvae (Barr, pers. comm.) | |
| | *Anthophora furcata* (Panzer) | 5–9 | E, S, common | various habitat areas | | |
| | *Andrena chrysosceles* (Kirby) | 3–6/7 | E, W, common | particularly associated with woodland | | |

## Results

The results of the evaluation are presented in Table 1. All model/mimic pairs or groups are regarded as prime candidates for more detailed investigation to determine whether the resemblance really is Batesian mimicry. For some model/mimic pairs there is much information additional to that given in Table 1, and these are discussed below. They are arranged according to the conclusions reached in the sequence social wasp mimics, solitary wasp mimics, bumble bee mimics, solitary bee mimics, hive bee mimics.

### Social wasp mimics

Pair No. 4. *Chrysotoxum arcuatum*, *C. cautum*, *C. elegans*, *C. octomaculatum* and *C. verralli* compared with *Dolichovespula* spp. and *Vespula* spp. (Plate 2).

*Chrysotoxum arcuatum* and *C. cautum* are the most commonly seen hoverflies of this group; they very closely resemble social wasps behaviourally and morphologically, with elongated antennae and colour patterns which are very wasp-like (e.g. Stubbs & Falk, 1983). The social wasps comprise *Vespula austriaca* (Panzer), *V. germanica* (F.), *V. rufa* (L.), *V. vulgaris* (L.), *Dolichovespula norwegica* (F.), and *D. sylvestris* (Scopoli). *Vespula austriaca* is a rare species which is a parasite in the nests of *Vespula rufa* (Chinery, 1986), but the other wasp species are all common and widespread. *Vespula* nest sites are usually subterranean whereas those of *Dolichovespula* are usually suspended from branches of trees or shrubs, or in hollow trees (Richards, 1980).

The flight of *Chrysotoxum* is similar to that of a wasp, and generally the only time it can be identified as not being a wasp is when it rests on vegetation (B.H., M.E. pers. observations). The flies are also found in the same habitat (see Table 1) and hence members of this group would seem to be Batesian mimics. The distribution of the two commoner species of this mimic group supports this view. *C. arcuatum* occurs north and west of a line from the Severn to the Humber, whereas *C. cautum* occurs south and east of this line (Stubbs & Falk, 1983; Ball & Morris, in preparation). Both species occupy the same flight season of May to September. Being allopatric means they will avoid being in competition with each other, but also means it is unlikely that the mimics will outnumber the models.

The hoverflies in this group vary in size, and another possible model species has been postulated for the smaller *C. arcuatum* (Table 1). *Anthidium* spp. are round and compact insects, a feature also shared by the hoverfly. There may be Müllerian mimicry between the social wasps and the bees from which the hoverfly would also benefit. However, *Anthidium* is not common in the north of Britain where *C. arcuatum* is widespread, but it is a possible model on continental Europe.

The hoverflies in this mimicry group have been classified in accordance with criteria (a), (b) and (c) as specific Batesian mimics of social wasps.

Pair No. 9. *Episyrphus balteatus* compared with *Nomada* spp.

Both species have slender bodies with yellow or orange and black markings, but although some *Nomada* spp. have a 'common' status, they never reach anything like the abundance of *E. balteatus*, which is often the commonest syrphid in mid and late summer. Although *E. balteatus* and *Nomada* are similar in size, colour and hovering behaviour, their detailed colour pattern is different, and they hover in different

**Plate 1** Top row: *Melanostoma mellinum*, *Crossocerus quadrimaculatus*; second row: *Brachypalpus laphriformis*, *Apis mellifera*; third row: *Mallota cimbiciformis*, *Criorhina asilica*; bottom row: *Brachypalpoides lenta*, *Astata boops*. Species in each row are to the same scale.

places. *Nomada* spp. are normally seen hovering low over the ground searching for prey species' nests, whereas *E. balteatus* is most often seen hovering near flowers or trees. Instead this hoverfly may benefit from a general resemblance to yellow and black social and solitary wasps, especially when it hovers and the details of its abdominal pattern are blurred. Although to human eyes *E. balteatus* appears rather unlike a wasp in colour and behaviour, to some birds the resemblance to wasps is very close (Dittrich *et al.*, 1993). It was therefore classified according to criterion (a) as a non-specific Batesian mimic of yellow and black solitary and social Hymenoptera.

Pair No. 14. *Syrphus* spp. compared with *Dolichovespula* spp. and *Vespula* spp.

The proposed mimics in this group include *Syrphus ribesii* (L.), *S. vitripennis* Meigen, *S. torvus* Osten-Sacken and various species of *Epistrophe*, *Parasyrphus* and *Metasyrphus*. All have yellow spots or bands across the otherwise black abdomen and so have some similarity to social wasps; but the size, shape and behaviour of the flies is so different to that of wasps that they were not initially included in Table 1 at all. However, they have wasp-like colours, and they are often the commonest hoverflies present, so it seems likely that they must gain some protection from their colour pattern. The hoverflies in this group have therefore been classified following criterion (a) as non-specific Batesian mimics of social wasps.

Pair No. 17. *Callicera aenea*, *C. rufa* and *C. spinolae* compared with *Osmia* spp., *Anthophora* spp. and *Eucera longicornis* (Plate 3).

Pinned specimens of these species of *Callicera* closely resemble the proposed models with similar shape, hairy bodies, and antennae. However, G. Rotheray (pers. comm.) has observed *C. spinolae* in the field. He reports that it is very like *Vespula* in flight and colour pattern, and flies with *Vespula* when feeding on ivy flowers. It has yellow bars across the abdomen which are very similar to those on *Vespula* when walking over flowers. It also folds its wings over the abdomen and even flicks them like a wasp. Finally its peak flight month is September when wasps are at their most abundant. *Callicera spinolae* has therefore been classified as a specific mimic of social wasps in accordance with criteria (a), (b) and (c). For the other species of *Callicera* further field observations are obviously required.

Pair No. 32. *Helophilus hybridus* Loew, *H. pendulus* (L.), *H. groenlandicus* (F.) and *H. trivittatus* (F.) mimicking *Dolichovespula* spp. and *Vespula* spp.

*Helophilus* spp. group comprises four hoverfly species which all resemble one another closely. Two of these, *H. hybridus* and *H. pendulus*, are common and widespread in a variety of habitats. To the human eye *Helophilus* spp. are poor mimics; when at rest the yellow and black colours are clearly visible, but the patterns are quite different from those of the suggested model species. *Helophilus* spp. also vary in size and do not display distinctive wasp-like morphological features such as long antennae.

Both *Helophilus* spp. and social wasps are very common throughout the British Isles (Chinery, 1986). *Helophilus* spp. are usually seen on flowers, or resting on ground vegetation. Social wasps occupy the same habitat niche with foraging trips including visits to flowers either for nectar or to find prey. Although *Helophilus* spp. have different markings to social wasps, their behaviour makes them appear much better mimics to the human eye. When disturbed from ground vegetation *Helophilus*

spp. fly forwards, sidewards, or upwards with 'jerky' movements (B. H. pers. observation). This 'distorts' their bold black and yellow colour patterns and the resemblance to a wasp is much more striking. Thus they appear most wasp-like when disturbed, perhaps by a predator, which is precisely when they are most in need of protection.

The *Helophilus* spp. group was classified according to criterion (a) as a non-specific Batesian mimic of social wasps because its black and yellow colour pattern is quite different from that of the model, but the flies probably gain some protection from resembling social wasps when in flight. This protection may be against insectivorous birds which have learned to avoid wasps, or alternatively, it might be against insectivorous insects such as social wasps where this behaviour and colour pattern may be a way of deceiving the wasp by imitating it.

Pair No. 42. *Sericomyia silentis* compared with *Dolichovespula* spp. and *Vespula* spp.

*Sericomyia silentis* is one of the larger hoverflies found in Britain. It is common and widespread, as is the model group (see pair No. 4, above, for notes of the model), and often found feeding on flowers in apparently unsuitable breeding habitats. When resting on a flower this hoverfly looks remarkably wasp-like with similar yellow and black markings on the abdomen which appears to be curved down (like that of a wasp) exposing yellow bands between the tergites, and the wings are dark and give the illusion of being folded (again like those of a wasp). It is larger than most other yellow and black syrphids, and its behaviour in flight is also similar to that of social wasps. In southern England and mainland Europe there are other social wasp mimics which are of similar size and even closer in appearance to social wasps (e.g. *Volucella inanis*), but in the rest of Britain this is the largest presumed social wasp mimic. *S. silentis* is most abundant from July till September which is also a time when social wasps are seen in large numbers, especially towards the end of the colony life. This hoverfly has been classified in accordance with criteria (a), (b) and (c) as a specific Batesian mimic.

## Solitary wasp mimics

Pair No. 1. *Baccha elongata* and *B. obscuripennis* compared with *Trypoxylon attenuatum* and *T. clavicerum*.

The proposed mimics are very slender, long-bodied flies which are often quite difficult to see (B.H. pers. observations). They are mainly found in woodlands and woodland margins, *B. obscuripennis* being the more common of the two (Stubbs & Falk, 1983). They can easily be mistaken for small wasps until inspected more closely. *Baccha* does not have long antennae, but it does have a very narrow waist typical of Hymenoptera. The proposed models are very similar morphologically and occur in the same habitat as the mimics (see Table 1) They also have similar distributions although the model is more commonly seen. These hoverflies have been classified in accordance with criteria (a), (b) and (c) as specific Batesian mimics.

Pair No. 2. *Melanostoma* spp. and *Platycheirus* spp. with yellow markings (also including *Melangyna lasiophthalma*) compared with *Crossocerus quadrimaculatus* (Plate 1).

This mimic group includes thirteen morphologically very similar hoverfly species: *Melanostoma mellinum* (L.), *M. scalare* (Fab.), *Melangyna lasiophthalma* (Zetterstedt),

**Plate 2** Top row: *Chrysotoxum arcuatum*, *Dolichovespula sylvestris*, *Anthidium* sp.; second row: *Parhelophilus frutetorum*, *Chrysotoxum cautum*, *Vespula rufa*; third row: *Dasysyrphus tricinctus*, *Nysson spinosus*; bottom row: *Doros profuges*, *Odynerus* sp.

**Plate 3** Top row: *Callicera spinolae*, *Osmia rufa*, *Eucera longicornis*; second row: *Lejops vittata*, *Coelioxys conoidea*, *Coelioxys* sp.; third row: *Scaeva pyrastri*, *Bembix rostrata*; bottom row: *Cheilosia chrysocoma*, *Andrena fulva*, *Osmia rufa*.

*Platycheirus angustatus* (Zetterstedt), *P. clypeatus* (Meigen), *P. fulviventris* (Macquart), *P. immarginatus* (Zetterstedt), *P. manicatus* (Meigen), *P. peltatus* (Meigen), *P. perpallidus* Verrall, *P. scambus* (Staeger), *P. scutatus* (Meigen) and *P. tarsalis* (Schummel). All are small slender hoverflies, black with yellow markings, which generally hover in woodland clearings, open grassland, marshes and moist grassland, and near flowers (Stubbs & Falk, 1983). Seven of these are common and widespread throughout much of the British Isles, two are southern species, one a northern species (Ball & Morris, in preparation), and three are considered scarce or rare. Such a large mimic group displays some variation in colour pattern, although on the wing they all look much the same (B.H., M.E. pers. observations). Most have a long flight period with only two species that show distinctive short seasons. In summary, this is a common group to be found in almost any type of habitat, sometimes congregating in large numbers, e.g. 50–100 (B.H. pers. observations), especially those species which are found in woodland margins.

*Crossocerus quadrimaculatus* is also common (although not as common as the hoverflies) and is small, with variable yellow markings (Richards, 1980). It is often seen amongst Diptera as it preys on them (Richards, 1980). The flies frequently hover between one and two metres in the air whereas *Crossocerus* is usually observed nearer the ground near its nest site.

The proposed model occurs mainly during June to August whereas the mimic group usually occurs from April to November, although it peaks from June to August. It is possible that predation is most prevalent during the peak months (this is when newly fledged birds are beginning to catch their own food), and therefore protection is gained at the time when the model is also on the wing. Alternatively, this mimic group has the ability of fast agile flight and therefore might not be as available to predators as alternative slower prey; its black and yellow coloration might then warn predatory birds that there would be no reward from pursuing such agile prey (Lindroth, 1971; Gibson, 1974, 1980).

We conclude that this group has a general resemblance to the proposed model (criterion (a)), but lacks the detailed morphological and behavioural similarities of criteria (b) and (c). It is therefore classified as a non-specific solitary wasp mimic.

### Bumble bee mimics

Pair No. 22. *Cheilosia illustrata* compared with *Andrena cineraria* and *Bombus pratorum*.

*Cheilosia illustrata* is a furry (densely hairy) fly with distinctive bands of white/buff and black on its thorax and abdomen, and with an orange tail. However, it varies in size and intensity of hue. In flight this species resembles the presumed models quite closely until it comes to rest (B.H., M.E. pers. observations). Unlike its proposed hymenopteran models, it spends much time sitting on umbel flowers feeding, but can also be found together with its models on blackthorn (*Prunus spinosa*) in April.

*A. cineraria* is a widely distributed Palaearctic species generally found throughout much of the British Isles (Else, in preparation), and is similar morphologically to *C. illustrata*. It can be found in a variety of habitats including pastureland, woodland, and chalk grassland, feeding on a variety of plants, including *Heracleum sphondylium* which is much visited by *C. illustrata* (Stubbs and Falk, 1983). *B. pratorum* occurs in the same habitat as the fly and includes workers which are as small as *C. illustrata*. Both species have an orange tail, furry body, and similar flight, but the detailed colour pattern is different. To the human eye *C. illustrata* does resemble a bumble bee,

particularly *B. pratorum*, although it can be mistaken for a small specimen of *B. terrestris*, particularly if the orange of the tail has faded. This indicates that *C. illustrata* may gain protection from generally resembling a furry solitary or social bee, and hence can be regarded as a non-specific Batesian mimic. In addition, its flight period coincides with that of the suggested models, peaking in abundance when both models are present (Howarth, 1998). This hoverfly has therefore been classified according to criterion (a) as a non-specific Batesian mimic.

Pair No. 30. *Eristalis intricarius* males compared with *Bombus pratorum*; females compared with *Bombus terrestris* and *B. lucorum*, and also with *B. lapidarius* and *B. ruderarius* (Plate 5).

*Eristalis intricarius* is sexually dimorphic and furry, with females appearing to our eyes much more like bumble bees than males. The males are generally black and orange possibly resembling workers of *Bombus pratorum*. The abdominal terga are usually dark but can have orange markings which are covered with hairs. Heal (1979) reports that some males fit the description of females, but we have not observed these in Lancashire. Males spend much time hovering when the orange hairs are particularly conspicuous. The males were classified in accordance with criterion (a) as non-specific Batesian mimics.

*Eristalis intricarius* females can occur in two forms, a black morph with a red tail, presumably mimicking *Bombus lapidarius* and *B. ruderarius*, and a black, yellow and white morph closely resembling *B. terrestris* and *B. lucorum* workers with an equally densely hairy body, similar markings, and similar body size. The peak flight period of presumed models and mimic are the same from June to September (Ball and Morris, in preparation; Prŷs-Jones and Corbet, 1987). Although the status of *E. intricarius* is 'common' it never occurs in large numbers and is found on the same food sources as the bumble bees (e.g. bramble). The hoverfly belongs to a genus which includes some of the most commonly seen hoverflies, yet it is quite different in appearance and behaviour, indicating a shift towards a more *Bombus*-like insect. The bumble bees tend to spend much time foraging and so the presumed model and mimic species can often be observed in close proximity. Although *E. intricarius* has a rat-tailed larva like other *Eristalis* spp. it is surprising that it is not seen more often. Female *E. intricarius* were classified according to criteria (a) and (b) as specific Batesian mimics of *Bombus terrestris* and *B. lucorum*, and also (the red-tailed morph) of *B. lapidarius* and *B. ruderarius*.

Pair No. 40. *Arctophila superbiens* mimicking *Bombus muscorum* and *B. pascuorum*.

The mimic is a large hairy fly which is coloured brown or orange, sometimes with a paler grey abdomen (B.H., M.E. pers. observations). It can easily be mistaken for an orange bumble bee as it frequents the same nectar source as its model and also peaks during the time of year when the models are particularly abundant (Howarth, 1998). To add to the morphological resemblance, *A. superbiens* closely mimics bumble bee flight, spending short periods of time on one flower head before 'bumbling' on to the next (Howarth, 1998). Unlike many hoverflies, when disturbed during feeding it does not exit with rapid flight but instead gently flies on to the next flower head, much the same behaviour that can be observed in *Bombus pascuorum*. *B. muscorum* and *B. pascuorum* resemble one another closely and are part of a Müllerian mimicry complex, with *B. pascuorum* being more common.

Many hoverflies are attracted by yellow (Disney *et al.*, 1982), and *Eristalis* species have been shown to extend the proboscis towards yellow anthers while being inhibited from feeding by blue and ultraviolet (Lunau, 1988; Lunau & Wacht, 1994), but *A. superbiens* feeds on purple knapweed (*Centaurea nigra*) and bluish devil's bit

**Plate 4** Top row: *Sericomyia lappona*, *Andrena flavipes*, *Andrena labialis*; second row: *Eristalis arbustorum*, *Stelis punctulatissima* male & female; third row: *Xanthogramma citrofasciatum*, *Nomada goodeniana*, *N. marshamella*; fourth row: *Xanthogramma pedissequum*, *Crabro cribrarius*, *Ectemnius* sp.; bottom row: *Pyrophaena granditarsa*, *Andrena labiata*, *Nomada fabriciana*.

**Plate 5** Top row: *Criorhina ranunculi* red-tailed morph, *Bombus lapidarius*, *Volucella bombylans*; second row: *Blera fallax*, *Osmia bicolor*; third row: *Volucella bombylans* var. *plumata*, *Eristalis intricarius*; fourth row: *Pocota personata*, *Bombus terrestris*; bottom row: *Eumerus tuberculatus*, *Stelis ornatula*.

scabious (*Succisa pratensis*) (Stubbs & Falk, 1983; Howarth, 1998). It seems likely that the mimicry of *A. superbiens* may include a physiological adaptation of the visual spectrum, as well as close morphological and behavioural resemblance. This hoverfly was classified according to criteria (a), (b) and (c) as a specific Batesian mimic of the proposed model group.

Pair No. 43. *Volucella bombylans* compared with *Bombus lapidarius*, *B. lucorum*, *B. ruderarius*, *B. terrestris*, and possibly *B. pascuorum* (Plate 5).

*Volucella bombylans* is very hairy with a broad abdomen, like a bumble bee, and is polymorphic. The typical form is black with a red tail presumably mimicking *Bombus lapidarius* and *B. ruderarius*; var. *plumata* has yellow, black and white bands and closely resembles *B. lucorum* and *B. terrestris*; and a rare brown morph appears to mimic *B. pascuorum*. The season is relatively short from May till August with a peak in June (Ball and Morris, in preparation). The fly has a 'common' status although it is rarely seen in large numbers. *V. bombylans* is associated with Hymenoptera as the larva lives in wasp nests where it is thought to scavenge or possibly be predatory on host larvae (Rotheray, 1993). The peak flight period of the *Bombus* spp. and of *V. bombylans* are the same (Howarth, 1998 for *V. bombylans*; Prŷs-Jones & Corbet, 1987 for *Bombus*). *V. bombylans* also has a similar 'bumbling' flight which adds to the close mimicry (B.H., M.E. pers. observations). *V. bombylans* was classified in accordance with criteria (a), (b) and (c) as a specific Batesian mimic.

Pair No. 53. *Criorhina berberina* compared with *Bombus pascuorum*, *B. pratorum*, and *B. terrestris*

*Criorhina berberina* is another densely hairy polymorphic syrphid with a black and buff banded morph (typical) presumably mimicking *Bombus terrestris* or possibly *B. pratorum*, and a brown morph, var. *oxyacanthae*, presumably mimicking *B. pascuorum*. This is the most frequently encountered of the *Criorhina* spp. (Ball and Morris, in preparation) commonly seen feeding on wild raspberry (*Rubus idaeus*) in the spring (B.H., M.E. pers observations). It is also the smallest of the *Criorhina* spp. and thus presumably a mimic of the bumble bee workers. It occurs from April till July, occasionally August, and there have been some sightings of this fly in September, indicating that it may be double brooded. The typical form is usually more frequent than var. *oxyacanthae*. This mirrors the abundance of the presumed model group as *B. terrestris* is more abundant in the spring with *B. pascuorum* at its peak in the autumn. The banded morph also resembles workers of *B. pratorum* because it is small and the bands are of equal size. The fly can often be observed feeding upside down which is a characteristic of *Bombus* spp., especially *B. pratorum*. *C. berberina* may be either a specific or a non-specific bumble bee mimic depending on the behaviour at the time. During feeding it resembles any small *Bombus* worker, but whilst at rest it more specifically resembles its respective presumed models. According to criteria (a), (b) and (c) this hoverfly is classified as a specific Batesian mimic.

Pair No. 55. *Criorhina ranunculi* compared with *Bombus lapidarius*, *B. lucorum*, *B. ruderarius*, and *B. terrestris* (Plate 5).

*Criorhina ranunculi* is a polymorphic species with two colour morphs, black with a red tail, presumably mimicking *B. lapidarius* and *B. ruderarius*, and black with a white or buff tail, presumably mimicking *B. lucorum* and *B. terrestris*. The hoverfly is large and hairy, the scutellum bearing slightly lighter bristles which gives the appearance of banding, as in many *Bombus* spp. In size it resembles queen bumble bees which are present at the same time; *C. ranunculi* is one of a few hoverflies found

at the beginning of the season utilising *Salix* spp. and blackthorn (*Prunus spinosa*) in March and early April, almost the only food sources available for the bumble bees at this time. To add to its morphological resemblance, *C. ranunculi* has a powerful flight, often 'bumping' into *Bombus* spp. a behaviour which could be interpreted as mate-searching (B.H. pers. observations). When caught in a net it appears to be very vicious, buzzing loudly in a *Bombus* fashion. This fly has been observed ovipositing in the afternoon at the base of trees during May (B.H. pers. observation). The models were actively collecting food from bluebells (*Scilla non-scripta*) whilst *C. ranunculi* was flying as low as the bees but landing on tree stumps and bases. The *Bombus* spp. can be found in a variety of habitats including woodlands where the mimic is present. The close morphological resemblance is greatly enhanced by the behaviour of *C. ranunculi* making it one of the most convincing specific Batesian mimics among the British fauna (classified according to criteria (a), (b) and (c)). During its flight period it occupies the canopy of its food source, hence close study is difficult, but essential for further understanding of any additional behavioural mimetic relationship.

### Solitary bee mimics

Pair No. 15. *Xanthogramma citrofasciatum* compared with *Nomada goodeniana*, *Nomada marshamella*, *Nomada fulvicornis*, and *Ectemnius* spp. (Plate 4).

*Xanthogramma citrofasciatum* is a brightly marked yellow and black hoverfly which can be observed hovering low over the ground. Like the presumed models it has bright orange legs. *Xanthogramma pedissequum* (pair No. 16, Plate 4) may also be a mimic of *Nomada* spp., but it has orange and black legs, much more similar to *Crabro cribrarius* and *Ectemnius* spp. than to *Nomada*. Many *Nomada* bees are similar in appearance, so they may be part of a Müllerian mimicry complex from which both *Xanthogramma* spp. benefit. *Xanthogramma citrofasciatum* and *Nomada* spp. were observed at one of the survey sites in very close proximity, both hovering low over the ground, occasionally making 'jerky' movements, and difficult to distinguish from one another. The flight period overlapped very closely (Howarth, 1998). According to criteria (a), (b) and (c), *X. citrofasciatum* is classified as a specific Batesian mimic of *Nomada* spp.

Pair No. 18. *Cheilosia albipila* compared with *Andrena apicata*.

This syrphid is one of a few hoverflies that occur very early in the season (Stubbs and Falk, 1983) and hence utilise one of the only food sources present at that time of year, catkins of *Salix* spp. It is dark with brown hairs on the abdomen. This fen, marsh and wet meadow species is usually found on sunny days (Stubbs and Falk, 1983). The presumed model species can also be found in these habitats although nesting in drier sand and chalk quarries. *A. apicata* occurs throughout most of the Palaearctic; it is widely distributed in southern Britain and Ireland (Else, in preparation), and has frequently been found on sampling trips in the north west region of the UK feeding on *Salix* spp. together with its presumed mimic (C.C. pers. observations). *C. albipila* has a slightly longer flight season but peaks during the flight period of the presumed model. Similarities in morphology, flight season and food source suggest that this is a specific Batesian model/mimic relationship, in accordance with criteria (a), (b) and (c).

Pair No. 21. *Cheilosia impressa*, *C. mutabilis*, *C. nebulosa*, *C. pagana*, and *C. vernalis* compared with *Lasioglossum albipes* and *L. fratellum*.

Both models and mimics are small, brown and shiny, and often occur on ground flowers. Although two bee species were identified, it is possible that other small bees in the genera *Halictus* and *Andrena* are part of this proposed model/mimic pair. These genera are often confused (Chinery, 1993), and before describing habitat and seasonal occurrence in detail, further study of this group is needed. This mimic group was classified in accordance with criterion (a) as non-specific Batesian mimics of the proposed model group.

### Hive bee mimics

Pair No. 29. *Eristalis arbustorum* compared with *Andrena flavipes*, *Stelis punctulatissima* and *Apis mellifera* (Plate 4).

This is one of the commonest British species of hoverflies, occurring in habitats varying from farmyards to open natural habitats (e.g. Stubbs and Falk, 1983). It is a large fly, very variable in colour (Holloway, 1993), and is widely classed as a bee mimic (Stubbs and Falk, 1983). However, Heal (1981) discusses sexual dimorphism where the females mimic several small, dark (mainly mining) bees, and the males less specifically mimic wasps and other yellow and black Hymenoptera. Because the males of this hoverfly have orange rather than yellow markings, they may also be honey bee mimics. *E. arbustorum* also resembles *Andrena flavipes* whose distribution is mainly southern and European, but the flight periods are the same (Else in preparation; Stubbs and Falk, 1983). The other suggested model, *Stelis punctulatissima*, is morphologically very similar to female *E. arbustorum*, but this is also a southern British species which does not occur frequently (Else, in preparation). Due to its large variability, *E. arbustorum* is classified according to criterion (a) as a non-specific Batesian Hymenoptera mimic. It would be interesting to compare colour variation found in Britain to that of other European districts, together with model frequencies.

Pair No. 31. *Eristalis pertinax*, *E. rupium* and *E. tenax* compared with *Apis mellifera*.

These three hoverflies (droneflies) are very similar to one another, although *Eristalis pertinax* usually has a more pointed abdomen, and all three species can vary in coloration. All three are widely accepted as being hive bee mimics (e.g. Gilbert, 1986; Stubbs and Falk, 1983). *E. rupium* is the least frequent syrphid of the group and its status is listed as 'notable' (Falk, 1991). *E. pertinax* and *E. tenax* are amongst the commonest hoverflies, widely distributed throughout the British Isles in many habitats. *Apis mellifera* is also found in most habitats and is often abundant, but not always as numerous as the *Eristalis* spp., and wild colonies are rarely observed in Britain. It is mainly a domesticated insect which has possibly increased its distribution and frequency since being farmed. Regardless of domestication, *A. mellifera* has been present in Britain, both wild and domesticated, for probably more than 1000 years. The effects of domestication of *A. mellifera* on the evolution of mimicry in the Syrphidae are unknown.

The mimic group also has some behavioural similarities in flight to honey bees. Honey bees can often be observed 'brushing' their legs in flight to collect any pollen. *Eristalis* spp. appear to move their legs in a similar fashion with no obvious function. This may be behavioural mimicry. The *Eristalis* spp. have therefore been classified according to criteria (a), (b) and (c) as specific Batesian mimics.

Pair No. 48. *Brachypalpus laphriformis* compared with *Apis mellifera* and *Colletes* spp. (Plate 1).

Although we have concluded that *Eristalis* spp. (pair no. 31) are specific honey bee mimics, *Brachypalpus laphriformis* and *Criorhina asilica* (pair nos 48 & 52) resemble honey bees even more closely. *Brachypalpus laphriformis* is a rarely encountered syrphid which has a 'notable' status (Falk, 1991). It is mainly found in the southern parts of Britain and is most frequent where there are areas with dead wood and in ancient forests. It has been seen in Lancashire but records are usually only one or two per season. The morphological resemblance is very precise, resembling the typical form of *A. mellifera*, whereas *Eristalis tenax*, *pertinax* and *rupium* (pair no. 31) resemble the introduced Italian variety. According to criteria (a), (b) and (c) the hoverfly has been classified as a specific Batesian mimic of *A. mellifera*.

A second model has been suggested due to the hairiness of the mimic. *Colletes succinctus* (L.) resembles *A. mellifera* although it is mostly found in sandy areas as it is ground-nesting. It occurs from July till September whereas the presumed mimic occurs from May till August. It is possible that *Colletes* spp. and honey bees are part of a Müllerian mimicry complex and that the hoverfly benefits from resembling several species of model.

Pair No. 52. *Criorhina asilica* mimicking *Apis mellifera* (Plate 1).

Morphologically *C. asilica* mimics *A. mellifera* closely except for the antennae. Personal observations have been mainly on wild raspberry in woodland clearings where it occurs together with its model. *C. asilica* is one of the rarer British hoverflies with saprophagous larvae which utilise decaying heartwood (Rotheray, 1993). The mimic has a very powerful flight and if disturbed at a food source will rapidly escape to the nearest woodland canopy (B.H. pers. observation). This mimic has been classified according to criteria (a), (b) and (c) as a specific Batesian mimic of *A. mellifera*.

## Discussion

The tentative matching of model/mimic pairs attempted here is not without problems. Although careful attention was paid to behaviour, in many cases behaviour of the model, mimic, or both has not been observed, and therefore matching can only be based on morphological and ecological evidence found in the literature, and on similarities observed in pinned museum specimens. The examples of *Episyrphus balteatus* and *Callicera spinolae* illustrate how conclusions as to which species is being mimicked based on museum material may be contradicted by field observations. Another example is the rare syrphid *Caliprobola speciosa* (pair no. 49), of which Raymond Uffen (pers. comm.) writes:

> "*Caliprobola speciosa* is a case of multifaceted mimicry and camouflage. It looks like nothing else, but you see it first as one thing, then another as it glints in the sun and seems to change shape and colour. True, its yellow-shaded wings and reflections off its abdominal hair bands can give the instantaneous impression of a wasp, but it has gone as soon as you or the fly move. When the sun goes in and a fly is left with its yellow wings closed, it is camouflaged sitting on rotten beech wood. With the wings splayed, the green body camouflages it in dull light on foliage. H. E. Hinton proposed that the brilliant, directionally reflective, structural colours of some ground beetles could confuse predators as the prey ran amongst vegetation on the ground, the colours now visible, now not, then changing. *Caliprobola speciosa* seems to be a chimera with an element of golden metallic glint superimposed on a cryptic

background. In a more restrained way than Hinton's beetles it lacks a visual identity."

*C. speciosa* clearly requires thorough ecological and behavioural investigation before its mimicry status can be confirmed.

It has been suggested that it would be helpful to categorise the 59 pairs according to the likelihood that they really are examples of mimicry (anonymous reviewer). However, our experience with *Episyrphus balteatus* and *Callicera spinolae* suggests that there may be several other pairs in which the hymenopteran most similar to the syrphid is not actually the model. Some flies may derive benefit from mimicking two quite different models, one which is comparatively rare or local (at least in this country) which they resemble very precisely, and the other which is common (perhaps a social species) which they resemble much less closely but sufficiently to give some protection. Only thorough experimental investigation will reveal if there is mimetic advantage to the hoverflies listed in Table 1.

It could be argued that by comparing two insect taxa which are both very diverse, pairs with similar colour patterns are almost sure to be found irrespective of whether mimicry is involved. However, a similar exercise with other families of Diptera such as the Muscidae would give very few matching pairs. It is probable therefore that many of the model/mimic pairs proposed here do indicate a mimetic relationship.

Another problem is the classification of colour and pattern. The human eye perceives colour in the visible spectrum of 400–700 nm (Wessells & Hopson, 1988). If mimicry is to be effective the mimic needs to copy the visual cues displayed by the model to confuse or deceive the predator. Recent research has shown that birds appear to be more sensitive to UV wavelengths (300–400 nm) than to the human-visible spectrum (Bennett & Cuthill, 1994). It may be the case that 'human' classification of flies and Hymenoptera into model/mimic pairs is not representative of how these species are perceived by the predators. Furthermore, with little evidence as to whether the main predators of hoverflies are birds (e.g. gull-billed tern *Gelochelidon nilotica*, Satheesan, 1990) or insects (e.g. the wasp *Ectemnius cavifrons*, Pickard, 1975), it is impossible to accurately describe what part of the mimicry is deceiving the predator: it could be morphology, behaviour, pheromones or a combination of any of these.

The examples of mimicry described here distinguish between non-specific mimics, which have a general similarity to the model, and specific mimics, which have a much closer resemblance in morphology, colour, pattern and behaviour. If specific mimics have evolved from non-specific mimics then one may also find mimics intermediate between these two categories in their degree of resemblance to the model. There must surely be a continuum between non-specific and specific mimics, the precise degree of similarity to the model depending on the perceptive abilities of the relevant predators: a hoverfly that is a poor morphological mimic may be a good behavioural mimic, and *vice versa*. Examination of Table I and the model-mimic pairs discussed above enable other conclusions to be drawn relating to generalist (non-specific) and specific mimics. Generalist mimics are common, occur in a variety of habitats, and have larval habits that do not restrict the flies to a narrow range of breeding habitats. Specific mimics are less common, occur in only some habitats (i.e. are local) and include some species whose larval habits restrict them to specific habitats. For example, *Syrphus* spp. are very common non-specific Batesian mimics, with a rather poor resemblance to wasps, occur in a wide variety of habitats, and have aphidophagous larvae; while *Criorhina* spp. are specific Batesian mimics, which are all highly accurate mimics to the human eye, and are restricted to semi-natural

ancient woodland because the larvae breed in dead wood (see Table 1). Table 2 summarises the conclusions as to which of the species discussed in this paper are likely to be specific mimics and which are non-specific mimics. It only lists the species discussed in detail together with *Criorhina floccosa* which has been observed in the field during the course of this study.

Bumble bees occur quite commonly in forests, woodland margins and clearings, and have habits which make them seem very numerous to a potential predator. Being social insects, bumble bees are frequently seen near their nest sites. The potential predator will encounter bumble bees frequently in such an area although very often they may be repeat sightings of the same individuals returning from foraging trips. The occasional specific mimic will presumably be difficult to distinguish from the model. The question arises: what and where are the predators against which mimicry has evolved? Wooded districts are likely to include bird predators nesting in the trees, and this may be the reason why many ancient woodland species are specific mimics. Maier (1978), who studied American syrphids, concluded that specialised mimics spend most of their life in forested areas where there is a high abundance of avian predators. Our data on specific British bumble bee mimics suggest that these too are predominantly woodland species.

Some of the syrphids which seem rather unconvincing mimics to the human eye may reflect UV (which humans cannot see) and thus may look much more like the model to potential predators. Dittrich *et al.* (1993) conducted experiments with photographic slides of several syrphids and model species. The reaction of pigeons to the slides showed that two common hoverflies which are non-specific yellow and black mimics, *Episyrphus balteatus* and *Syrphus ribesii*, were ranked as very similar to the wasps shown to the pigeons although neither is especially wasp-like to human eyes. Cuthill & Bennett (1993) argued that the differences between avian and primate colour vision were responsible for the categorisation of the pigeons as the slides were designed for human vision and therefore lacked the natural colour information which wild birds perceive, especially UV. This would explain why the museum-based comparison in Table 1 showed *E. balteatus* as being a mimic of *Nomada* instead of wasps.

Many of the proposed mimics resemble social Hymenoptera or large solitary wasps (e.g. *Ectemnius* spp.) which have stings that are painful to humans and to some birds. Such birds will learn to avoid the models and may then be deceived into ignoring the mimics. Other proposed mimics resemble small species of solitary bee or wasp whose stings are much less virulent, at least to humans. The question then arises of whether a predator would find these hymenopterans unpleasant: if not then there can be no advantage in a hoverfly mimicking them. However, the solitary wasps which prey on insects or spiders are likely to have stings that are effective against insect predators, so it may pay a syrphid to mimic these wasps. Many of the smaller hymenopterans are also very agile in flight and may be difficult for predators to catch. Predators may then learn that it is not profitable to chase them. Small syrphids that resemble such hymenopterans could be Batesian or Müllerian mimics (Edmunds, 1974; Gibson, 1974, 1980).

Some of the model/mimic pairs described above have different spatial distributions. In most cases all species proposed as a pair are fairly mobile and will forage for food in a variety of habitats so that co-occurrence between model and mimic will take place. However, there are some pairs suggested above that are very unlikely to occupy the same habitats, e.g. pair no. 46. *Blera fallax*, apart from not being hairy, resembles the model group closely in morphology and seasonal flight period (Plate 5). In Britain this rare hoverfly only occurs in east Scotland whereas the model is a

Table 2. Tentative conclusions as to the nature of the Batesian mimicry of hoverflies discussed in the text.

| No. | Hoverfly (above) and Proposed Model Species (below) | Conclusion |
|---|---|---|
| 1. | *Baccha elongata*, *B. obscuripennis*<br>*Trypoxylon attenuatum*, *T. clavicerum* | Specific mimic |
| 2. | *Melanostoma* spp., *Platycheirus* spp. with yellow markings<br>*Crossocerus quadrimaculatus* | Non-specific mimic |
| 4. | *Chrysotoxum arcuatum*, *C. cautum*, *C. elegans*, *C. octomaculatum*, *C. verralli*<br>*Dolichovespula* spp. and *Vespula* spp., *Anthidium* spp. | Specific mimic |
| 9. | *Episyrphus balteatus*<br>*Nomada* spp. | Non-specific mimic of black & yellow wasps |
| 14. | *Syrphus* spp.<br>*Dolichovespula* spp. and *Vespula* spp. | Non-specific mimic |
| 15. | *Xanthogramma citrofasciatum*<br>*Nomada goodeniana*, *N. marshamella*, *N. fulvicornis*, *Ectemnius* spp. | Specific mimic |
| 16. | *Xanthogramma pedissequum*<br>*Crabro cribrarius*, *Ectemnius* spp., *Nomada* spp. | Specific mimic |
| 17. | *Callicera aenea*, *C. rufa*, *C. spinolae*<br>*Osmia* spp., *Anthophora* spp., *Eucera longicornis* | Specific mimic of social wasps |
| 18. | *Cheilosia albipila*<br>*Andrena apicata* | Specific mimic |
| 21. | *Cheilosia impressa*, *C. mutabilis*, *C. nebulosa*, *C. pagana*, *C. vernalis*<br>*Lasioglossum albipes*, *L. fratellum* | Non-specific mimic |
| 22. | *Cheilosia illustrata*<br>*Andrena cineraria*, *Bombus pratorum* | Non-specific mimic |
| 29. | *Eristalis arbustorum*<br>*Apis mellifera*, *Andrena flavipes*, *Stelis punctulatissima* | Non-specific mimic |
| 30. | *Eristalis intricarius*<br>*Bombus terrestris*, *Bombus pratorum* | Female: specific mimic; male: non-specific mimic |
| 31. | *Eristalis pertinax*, *E. rupium*, *E. tenax*<br>*Apis mellifera* | Specific mimic |
| 32. | *Helophilus* spp.<br>*Dolichovespula* spp. and *Vespula* spp. | Non-specific mimic |
| 40. | *Arctophila superbiens*<br>*Bombus muscorum*, *B. pascuorum* | Specific mimic |
| 42. | *Sericomyia silentis*<br>*Dolichovespula* and *Vespula* spp. | Specific mimic |
| 43. | *Volucella bombylans*<br>*Bombus lapidarius*, *B. lucorum*, *B. ruderarius*, *B. terrestris*, and possibly *B. pascuorum* (pale variety) | Specific mimic |
| 48. | *Brachypalpus laphriformis*<br>*Colletes* spp., *Apis mellifera* | Specific mimic |
| 52. | *Criorhina asilica*<br>*Apis mellifera* | Specific mimic |
| 53. | *Criorhina berberina*<br>*Bombus pascuorum*, *B. pratorum*, *B. terrestris* | Specific mimic |
| 54. | *Criorhina floccosa*<br>*Bombus muscorum*, *B. pascuorum* | Specific mimic |
| 55. | *Criorhina ranunculi*<br>*Bombus lapidarius*, *B. lucorum*, *B. ruderarius*, *B. terrestris* | Specific mimic |

southern and European species. In Europe the hoverfly is much commoner. Avian predators are very mobile and many are migratory. It is possible that bird predators would have learned to avoid the models of *Blera fallax* during migration. Avoidance learning of models and mimics by birds could occur in several ways: the bird (a) encounters and learns to avoid both model and mimic in the same area; (b) learns to avoid the model in one place, migrates, and then avoids the mimic in another place; (c) learns to avoid the model in one place, migrates, and remembers to avoid both model and mimic on its return (Waldbauer, 1988 and earlier, concludes that birds in the United States behave as in (c)).

Another example of differing spatial distribution is pair no. 12, *Scaeva pyrastri* and *Bembix rostrata* (Plate 3). There is close morphological resemblance between these two species, including size, pattern of white markings on the abdomen, yellow legs and a very similar head shape and coloration. Although *S. pyrastri* appears as a British hoverfly, its status is a 'migrant' which reaches the British Isles in June/July from southern Europe (Ball & Morris, in preparation). *Bembix rostrata* is a European species, thus it is likely that this is a Batesian mimicry relationship. The migratory nature of this hoverfly is more than likely due to its larval feeding habits on ground layer and arboreal aphids which are also known to migrate. How the Batesian mimicry of *S. pyrastri* is maintained when it is away from its proposed model may be better understood if the predators were known.

It is indisputable that many hoverflies closely resemble certain Hymenoptera, and so it seems probable that many of them gain protection from this resemblance. Table 1 proposes 59 possible model/mimic pairs, but only a thorough investigation of the behaviour of these pairs will support or refute these proposals.

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## SHORT COMMUNICATION

***Conocephalus discolor* (Thunberg) (Orthoptera: Tettigoniidae) new to Wales.**—During a survey on 15.viii.1999 by members of the Cardiff Naturalists' Society, of the wildlife within a large road interchange (M4 Junction 32) at Coryton on the northern outskirts of Cardiff, we discovered a colony of *Conocephalus discolor* (long-winged cone-heads). A further visit a few days later confirmed that nymphs, adult males and especially adult females of this species were present on at least three separate parts of the interchange. The site (ST140816) is the area within the M4/A470 interchange, about 10 hectares of rough grassland, shrubs and trees. The cone-heads were found in areas of damp grassland.

Since the early 1980s this species has expanded its range northwards from the south coast of England (Marshall & Haes, 1988; Haes & Harding, 1997; Widgery, 1999). This is considered to be as a result of climate change (global warming). Although few records of Welsh Orthoptera have been submitted recently to the National Orthoptera Recording Scheme, the nearest previous sightings are some distance away—65 km to the south in Somerset and 85 km to the east in Gloucestershire (J. Widgery, *pers comm.*). The site's proximity to the M4 raises intriguing questions about the means and source of colonisation.

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